

Some Problems in the Systematics of the Order Scolopendromorpha (Chilopoda)

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ABSTRACT

The class Chilopoda ought to be divided into Noto- and Pleurostigmophora in relation to its phylogeny. It is hard to speak about poly- vs. oligomerization as a general pathway in the evolution of the Chilopoda as a whole, chiefly due to an extremely early isolation of the Scutigermorpha and a polymeric development in the Geophilomorpha. The family Cryptopsidae (Scolopendromorpha) is an unnatural composite taxon because of its polyphyly. This is easily to explain in terms of the theory of biological progress associated in all branches of scolopendromorphs with a transition to a hypogean mode of life.

RÉSUMÉ

Quelques questions de systématique dans l'ordre Scolopendromorpha (Chilopoda).

La classe Chilopoda devrait être divisée, d'après sa phylogénie, en Noto- et Pleurostigmophora. Il est difficile de considérer le contraste "polymétamérisation - oligométamérisation" comme une voie générale de l'évolution de l'ensemble Chilopoda, principalement à cause de l'isolement extrêmement précoce des Scutigermorpha et du développement "polymétamérique" des Geophilomorpha. La famille Cryptopsidae (Scolopendromorpha) apparaît comme un taxon composite non-naturel à cause de sa polyphylie. Ceci est assez facile à expliquer en théorie par l'association, dans toutes les lignées de scolopendromorphes, d'une évolution biologique et d'une transition vers un mode de vie hypogé.

INTRODUCTION

Chilopod evolution is a subject of active debate (e.g. MANTON, 1952; PRUNESCU, 1965; SHINOHARA, 1970; DOHLE, 1988; SHEAR & BONAMO, 1988). Basically, some studies adhere to oligomerization (= reduction in the number of body segments) as the major evolutionary trend in the Chilopoda, while others document that in terms of polymerization. Systematically, the class has been divided either into Noto- and Pleurostigmophora or Ana- and Epimorpha, dependent on the pattern of allocation of the stigmata and the traits of postembryonic development, respectively. (By the way, is such a character as the type of development (ana- vs. epimorphosis) reliable taxonomically for dividing taxa of so high level?).

However, in addition to new evidence accumulated in the recent years, particularly the discovery of a new extinct chilopod order (SHEAR & BONAMO, 1988), and a new cladistic analysis (DOHLE, 1988), much remains to be clarified, either based on recent results or older literature data.

The main impetus for presenting this preliminary paper lies in the deep interest we can find, among Chilopoda, in the evolution and systematics of the order Scolopendromorpha (e.g. SCHILEYKO, 1992; ZALESSKAJA & SCHILEYKO, 1992).

SYSTEM OF THE SCOLOPENDROMORPHA

At present, the system of ATTEMS (1930) of the centipede order Scolopendromorpha is generally accepted, with such characters as the presence or absence of eyes serving as its basis. The order is divided into two families: Scolopendridae (16 genera with eyes) and Cryptopsidae (12 blind genera) (Fig.1). However, about five years ago, when working with a collection of *Scolopocryptops ferrugineus* (Brölemann, 1919), from Cuba, I found great similarity between *Scolopocryptops* Porat, 1876 and numerous Scolopendridae. In addition, I noted many differences between *Scolopocryptops* and *Cryptops* Leach, 1815 (Fig.1). This provoked the conclusion that Cryptopsidae is possibly a polyphyletic group. In other words, the main reason for revising the system of this order is the apparent polyphyly of the family Cryptopsidae.

To my mind, the Attemsian system seems to reflect the order's eco-morphology rather than phylogeny and fails to explain the allocation within a monophyletic family Cryptopsidae of such quite different representatives as the genera *Scolopocryptops*, *Dinocryptops* Newport, 1844, *Plutonium* Cavanna, 1881 or *Cryptops* (Fig. 1), regardless of the pathway centipede evolution we accept (oligo- vs. polymerization).

I have therefore analyzed all available material from the Zoological Museums of Moscow and St-Petersburg. This amounted to about two thousand specimens from the following genera (Fig. 1): *Theatops* Newport, 1845, *Tonkinodentus* Schileyko, 1992, *Cryptops*, *Paracryptops* Pocock, 1891, *Scolopocryptops*, *Dinocryptops*, *Newportia* (all Cryptopsidae), and *Scolopendra* L., 1758, *Cormocephalus* Newport, 1844, *Asanada* Meinert, 1886, *Otostigmus* Porat, 1876, *Alipes* Imhoff, 1845, *Ethmostigmus* Newport, 1845, *Rhysida* Newport, 1845 (all Scolopendridae).

I have tried to evaluate the maximal number of characters, the main of which are the following (Table 1):

(1) number of spiracles; (2) number of body segments; (3) structure of spiracles; (4) presence of eyes; (5) presence of tooth plates of maxillipede coxosternite; (6) presence of coxopleural pores; (7) presence of coxopleural process; (8) structure and ornament of last legs.

Plesiomorphy is coded by 0, apomorphy by 1 and serial transformations by 2 to 4 (Table 1).

TABLE 1. — List of the characters with their evaluation as apomorphy or plesiomorphy.

Characters	Plesiomorphic	Apomorphic
1. Number of spiracle pairs	19 (0)	11 (1), 10 (2), 9 (3)
2. Number of body segments	23 (0)	21 (1)
3. Structure of spiracles	without flap (0)	with flap (1)
4. Eyes	presence (0)	absence (1)
5. Tooth plates	presence (0)	absence (1)
6. Coxopleural pores	presence (0)	absence (1)
7. Coxopleural process	presence (0)	absence (1)
8. Structure of last legs	pincer-shaped, without spines (0)	normal-shaped, with spines (1), leaf-shaped (2), with "saw" (3), many-segmented tarsi (4)

However, I have not attempted a cladogram, because I have not seen representatives of all genera. A cladogram, in this case, would be deficient. Besides, to my mind, the cladistic methods are sometimes not objective, because the choice of characters, the evaluation of degree

of their expression and of their taxonomical importance is rather subjective (same as in the "classic" methods). Because of all this, certainly the set of characters to be analyzed must be extended.

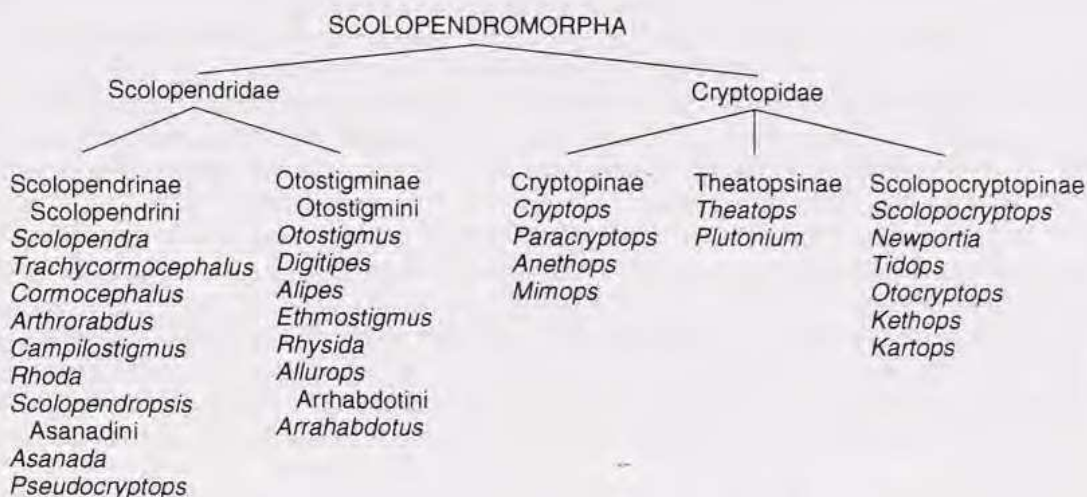


FIG. 1. — System of the Scolopendromorpha after ATTEMS (1930).

A character matrix has been compiled (Table 2). *Plutonium* is a single genus, which I have never personally seen, but I included it in the matrix, because of the great importance of this form for phylogeny of the whole Scolopendromorpha. I analyzed the cardinal character of the system of ATTEMS. To my mind, this character is highly adaptive and not reliable taxonomically. There are numerous examples of eye losses in connection with the transition to a hypogeal mode of life (edaphic and cavernicolous), e.g. in some Lithobiidae centipedes, Atyidae shrimps, Trigonochlamydidae slugs, Characinidae fishes, etc.

Closely related forms with eyes are always present.

The system of ATTEMS is based on a single character. In this case, if one of that two families is polyphyletic, all the system is not reliable. In my opinion, this matrix demonstrates that Cryptopsidae, sensu ATTEMS, is not monophyletic (Table 2).

TABLE 2. — The matrix of the characters.

Genus		Characters							
		1	2	3	4	5	6	7	8
Cryptopsidae	<i>Plutonium</i>	0	1	0	1	0	0	0	0
	<i>Theatops</i>	3	1	0	1	0	0	1	0
	<i>Tonkinodentus</i>	3	1	0	1	0	0	0	?
	<i>Cryptops</i>	3	1	0	1	1	0	1	3
	<i>Paracryptops</i>	3	1	0	1	1	0	1	3
	<i>Scolopocryptops</i>	1	0	0	1	0	0	0	1
	<i>Otocryptops</i>	2	0	0	1	0	0	0	1
	<i>Newportia</i>	1	0	0	1	0	0	0	4
Scolopendridae	<i>Scolopendra</i>	3	1	1	0	0	0	0	1
	<i>Cormocephalus</i>	3	1	1	0	0	0	0	1
	<i>Asanada</i>	3	1	1	0	0	1	1	1
	<i>Otostigmus</i>	3	1	0	0	0	0	0	1
	<i>Alipes</i>	3	1	0	0	0	0	0	2
	<i>Ethmostigmus</i>	2	1	0	0	0	0	0	1
	<i>Rhysida</i>	2	1	0	0	0	0	0	1

In addition, there is a very interesting question about the monotypical genus *Plutonium*, which has 21 body segments with 19 pairs of spiracles, in other words the spiracles are disposed on all body segments, except for the first and the last one (as in Geophilomorpha). As I have already written, the Attemsian system fails to explain the allocation within the family Cryptopsidae of some very morphologically different genera, and at first the allocation of *Plutonium zwierlainii* Cavanna, 1881, regardless of the apo- or plesiomorph type of its homonymity. Some of my ideas about the last problem are as follows.

The evolution of most groups of polymerous invertebrates, which left the soil environment for surface habitats, is known to have undergone oligomerization (Arachnida, Insecta). In my opinion, it is difficult to speak about poly- vs. oligomerization as a general pathway in the evolution of the Chilopoda as a whole, primarily due to an extremely early isolation of the Scutigermomorpha and a polymerous development in the Geophilomorpha. However, it is known that the reduction of spiracles is associated with the development of anisotery at first, and this takes place in all orders of the Chilopoda which have moved to open habitats.

By the way, a second possible reason for this reduction is apparently connected with a reduced transpiration rate through these structures devoid of epicuticle (KAUFMAN, 1959). Water economy could have become more important during chilopod penetration into arid habitats and regions. The dorso-medial spiracles of Scutigermomorpha are, possibly, the top of evolution of this structure.

But representatives of Geophilomorpha have moved to the hypogean mode of life and have a homonomous and polymerous body without well expressed anisosegmentation. Their polymerization can be easily explained in terms of adaptation to active wormlike movements in a more dense environment. But if the homonymity in Geophilomorpha is an apomorphy, I cannot clearly imagine what their evolutionary pathway was, assuming so because their ancestor had an anisosegmentation. But as an alternative, the Geophilomorpha could have had a homonomous ancestor, and they retained homonymity.

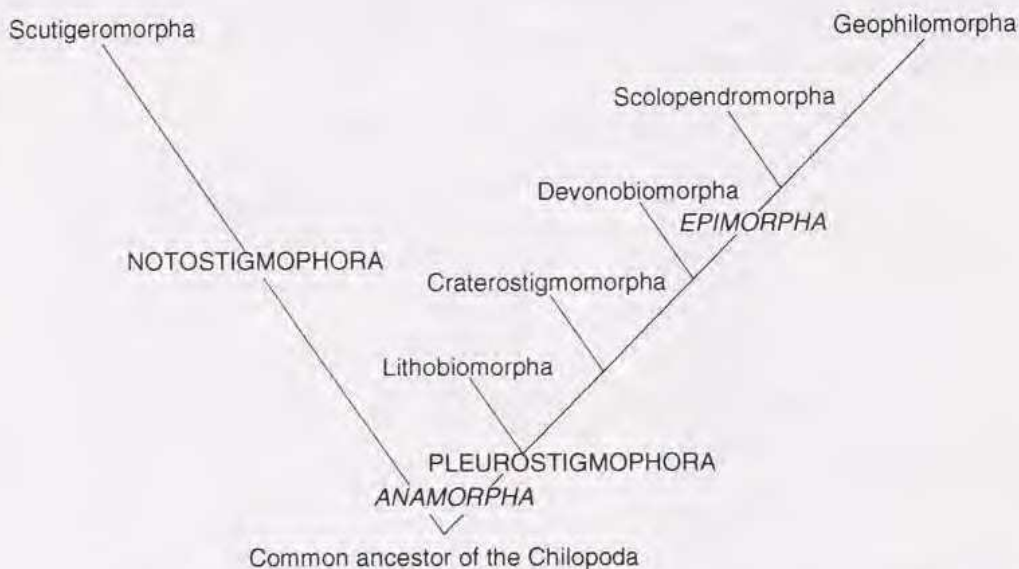


FIG. 2. — The phylogenetic tree of the Chilopoda after SHEAR & BONAMO (1988).

Moreover, the Scolopendromorpha and the Geophilomorpha are closely related groups (PRUNESCU, 1965; DOHLE, 1988; SHEAR & BONAMO, 1988) (Fig. 2) and most probably have a common ancestor. In this case, if body homonomy is a plesiomorphy in the Scolopendromorpha, their ancestor would have had a homonomous body. However, anisotergy would have been absolutely mandatory for groups of centipedes which colonized the soil surface. Anisosegmentation is gradually increasing in the following row: Scolopendromorpha - Craterostigmomorpha - Lithobiomorpha - Scutigermomorpha. Apparently, this fact is due to an increased velocity and manoeuvrability while moving and improving the transpiratory system. All these are especially important for predators. I note that this succession is not an evolutionary one, but it is only an attempt to a morpho-functional analysis of anisosegmentation.

CONCLUSIONS

1. So the family Cryptopidae (*sensu* ATTEMS) is probably an unnatural composite taxon, because of its polyphyly. This is easily explicable in terms of the theory of biological progress, associated in all groups of scolopendromorphs with a transition to a hypogean mode of life.

2. If the homonomy is plesiomorphic in the Scolopendromorpha, *Plutonium* is a form most closely related to their common ancestor. Hence, perhaps *Plutonium* deserves not only a family of its own (SCHILEYKO, 1992), but even a suprafamily status, as an absolutely different group.

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REFERENCES

- ATTEMS, G., 1930. — *Myriapoda. 2. Scolopendromorpha*. In : *Das Tierreich*. Berlin, Walter de Gruyter & Co, 307 pp.
- DOHLE, W., 1988. — *Myriapoda and the Ancestry of Insects*. Manchester, Impact Print Services Ltd., 28 pp.
- KAUFMAN, Z. S., 1959. — Morphology of spiracles of *Geophilus proximus* C. L. Koch (Chilopoda). *Dokl. AN USSR*, **129** : 698-701. (in Russian).
- MANTON, S. M., 1952. — The evolution of Arthropodan locomotory mechanisms. Part 2. General introduction to the locomotory mechanisms of the Arthropoda. *J. Linn. Soc. (Zool.)*, **42** : 93-167.
- PRUNESCU, C. C., 1965. — Contribution à l'étude de l'évolution des Chilopodes. *Rev. Roum. Biol. (Zool.)*, **10** : 89-102.
- SCHILEYKO, A. A. JR., 1992. — Scolopenders of Viet-Nam and some aspects of the system of Scolopendromorpha (Chilopoda Epimorpha). Part 1. *Arthropoda Selecta*, **1** : 5-19.
- SHEAR, W. A. & BONAMO, P. M., 1988. — Devonobiomorpha, a new order of centipedes (Chilopoda) from the middle Devonian of Gilboa, New York State, USA, and the phylogeny of Centiped Orders. *Amer. Mus. Nov.*, **2977** : 1-30.
- SHINOHARA, K., 1970. — On the phylogeny of Chilopoda. *Proc. Japan. Soc. Syst. Zool.*, **65** : 35-42.
- ZALESKAJA, N. T. & SCHILEYKO, A. A. JR., 1992. — *The scolopendromorph centipedes of USSR*. Moscow, "Nauka" Publ., 110 pp. (in Russian).